# SISYRINCHIUM SOLSTITIALE (IRIDACEAE): A FLORIDA ENDEMIC

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NUMEROUS SPECIES OF *Sisyrinchium* from the southeastern United States were described by Bicknell (1899). Many of these have been placed in synonymy or ignored because of their uncertain status. Included among these is *S. solstitiale*, which is similar to, and usually included within, *S. xerophyllum* Greene. In the original publication of the former species, Bicknell emphasized the different flowering times of these species (autumnal in *S. solstitiale*, vernal in *S. xerophyllum*) and later (1903) stated that in *S. xerophyllum* the tufts of plants are densely fibrous at the base, while in *S. solstitiale* such fibers are lacking. The amount and condition of fibers depends on the age of the plant, fires, and microhabitat and does not distinguish these species. We believe that not recognizing this has led to the inclusion of *Sisyrinchium solstitiale* in *S. xerophyllum* in recent treatments of the genus in Florida (Lakela & Craighead, 1965; Ward, 1968; Long & Lakela, 1971).

After two years of observing living populations of *Sisyrinchium* in peninsular Florida, of collecting data on pollinators, phenology, habitat, cytology, and of examining numerous herbarium specimens, it became apparent that the entity called "*S. xerophyllum*" in recent literature was composed of two distinct, yet closely related, taxa. Historically, few infraspecific taxa of *Sisyrinchium* have been recognized in North America. Until a clear species concept can be established through detailed population and biosystematic studies, we prefer to follow the present system and maintain *S. xerophyllum* and *S. solstitiale* as distinct species. TABLE I lists the characters that may be used to distinguish them.

The genus *Sisyrinchium* is taxonomically difficult; species limits are often vague, and many variants have been described as distinct. Numerous collections in herbaria are undetermined or misdetermined. Taxonomic studies on the genus are few and based mostly on herbarium material. They are mostly regional in coverage or concerned with small species groups. A modern revision is needed.

## ECOLOGY

*Sisyrinchium solstitiale* and *S. xerophyllum* are closely allied species which were probably derived relatively recently from a common ancestor. *Sisyrinchium solstitiale* is adapted to the xeric conditions of the Scrub Pinelands, and *S. xerophyllum* to the comparatively mesic conditions of the High Pinelands. The distribution of these species (FIGURE 5) apparently reflects the Pleistocene insulation and inundation described

TABLE I. **Criteria for distinguishing Sisyrinchium solstitiale from S. xerophyllum.**

| S. SOLSTITIALE | S. XEROPHYLLUM |
|---|---|
| 1. Scapes 30–54 cm. long. | Scapes 7–25(–30) cm. long. |
| 2. Inflorescences 12.5–23 cm. long; 3.5–9.5 cm. longer than the leafy bract. | Inflorescences 4–8 cm. long; up to 3 cm. longer than the leafy bract. |
| 3. Spathes ± terete at base, gradually broadening. | Spathes flattened, abruptly expanding from base. |
| 4. Outer bract gradually tapering to a point. | Outer bract abruptly narrowing from point of attachment. |
| 5. Inner bract not gibbous. | Inner bract slightly gibbous. |
| 6. Pedicels (0–)5–7(–10) mm. longer than spathes. | Pedicels (0–)2(–6) mm. longer than spathes. |
| 7. Roots commonly pilose (root hairs?). | Roots commonly smooth. |
| 8. Habitat: Scrub. | Habitat: High Pine and Flatwoods. |
| 9. Flowering July to December. | Flowering March to April. |
| 10. Leaves evergreen, persistent throughout year. | Leaves dying in the fall. |

by Neill (1957) for numerous species of plants and animals. *Sisyrinchium solstitiale* now grows on the Ocala Ridge from Marion County south to Highlands County and southeast on the Scrub Pine sand dunes to Dade County. Where the species occurs in Pine Flatwoods it has been our observation that a "relic" of Scrub Pinewoods is always closely associated.

With the exception of the collection *Nash 133*, *S. xerophyllum* occurs north of the Suwanee Straits from Alachua and Putnam counties north to Duval County. It appears to be absent from the Suwanee River basin, but reappears in the panhandle from Leon to Walton counties. This absence from the Suwanee River basin is probably a result of the inundation of this region during the Pleistocene. Neill (1957) described in detail the effect of the embayment on local biogeography and noted that many species of plants and animals have not yet reinhabited the area.

*Sisyrinchium solstitiale* is constantly associated with the white St. Lucie and associated cross-bedded sands of the Pleistocene (Cook, 1945). Vegetation growing on this sand complex is usually called Scrub or Scrub Pine (Carr, 1940; Davis, 1943; Long & Lakela, 1971) and is characterized by the dominant plants *Pinus clausa*, *Ceratiola ericoides*, and several species of *Quercus*. In *Pinus clausa* stands having a closed canopy and thick shrub layers, *S. solstitiale* is not apparent even after fires. Conversely, scrub pine stands with an open canopy are common sites of large *Sisyrinchium* populations. Following fires that do not kill the scrub

pine, large *Sisyrinchium* populations are abundant in open areas. Roads and trails leading through or near such populations allow the spread of a few plants into nearby High Pinelands or Flatwoods. *Sisyrinchium solstitiale* appears unable to compete with *Serenoa repens* (saw palmetto), ericaceous shrubs, and grasses common in the High Pinelands and Flatwoods. In southern Florida *S. solstitiale* is found only in young Flatwoods and their disturbed margins, and only then when there is a Scrub area nearby. When the lower pine forest layers begin to mature *Sisyrinchium* becomes rare or absent.

This perennial *Sisyrinchium* may not be adapted to fire in the same ways that *Serenoa*, *Quercus*, *Lyonia*, and *Ilex* are adapted, but, as with many Florida plants, it benefits from reduced competition, release of nutrients, and the preparation of the proper habitat for growth and reproduction. The species possibly exists marginally for long periods of time until fire reduces competition and thus opens and maintains a suitable habitat.

The genus *Sisyrinchium* is largely one of temperate regions, although some species extend into tropical zones. Those species in the tropics usually occur at higher altitudes where conditions are functionally temperate. Most species of the north temperate area flower in the spring and early summer.

*Sisyrinchium solstitiale* rarely produces flowers in the spring; of the several hundred living plants examined in March, 1972, only two plants had one flower each. These same plants had flowering stalks with capsules that had already dispersed their seed. Observations during three seasons of one population in Palm Beach County and another in Martin County, plus data from herbarium material indicate that the majority of *S. solstitiale* flowers are produced from July to December.

From greenhouse studies it has been determined that flowering is initiated by photoperiod in some *Sisyrinchium* species (Oliver, unpublished). This photoperiod sensitivity undoubtedly has partially dictated the time of year when *S. solstitiale* produces flowers. Spring and fall flowering appear to reach their peak near the equinoxes when there are about twelve hours of light. The production of occasional flowers by *S. solstitiale* in the spring suggests that flowering is at least partially triggered by photoperiod.

However important photoperiod might be in initiating flowering, moisture seems to be one of the main factors affecting the change from spring to late summer and fall flowering. Spring is almost always dry in peninsular Florida, while fall terminates the wet season. Since the spring drought is augmented by the very porous well-drained sand soils where *S. solstitiale* occurs, this may have become a factor limiting spring flowering of this species. Spring flowering for *S. solstitiale* must have become an evolutionary handicap, and selection caused a shift to fall flowering. A similar fall flowering tendency is exhibited by numerous Mexican species of the genus that begin flowering in July and August. This also corresponds with the rainy season.

## POLLINATION

Two widely separated populations of *S. solstitiale* have been observed for insect visitors. Although several kinds of insects were seen in the vicinity of the populations, only three species of Hymenoptera visited *Sisyrinchium*.

In the Boca Raton, Palm Beach County population, flowers opened from 2:30 to 3:00 p.m. E.S.T. and remained open until after dark. The afternoon flowering appears to be a unique characteristic of *S. solstitiale*; other species of the genus flower in the morning. Bees were not apparent until the flowers opened. Shortly after opening the flowers were visited by *Augochlorella gratiosa* Smith and *Anthidiellum notatum rufimaculatum* Schwarz. *Augochlorella* was a regular visitor for the next few hours, at least one bee visiting the flowers at all times. The body of *Augochlorella* was positioned across or around the staminal column for gathering nectar (FIGURES 3 and 4). Pollen was collected with the anterior pair of legs after nectar had been taken, and then stored in scopae on the posterior legs.

*Anthidiellum*, a larger bee, landed across the staminal column to take nectar at the flower base while gathering pollen at the same time with the posterior legs. This bee stores pollen on ventral abdominal scopae. Although there is no detectable fragrance, these bees always approach the flowers from down-wind.

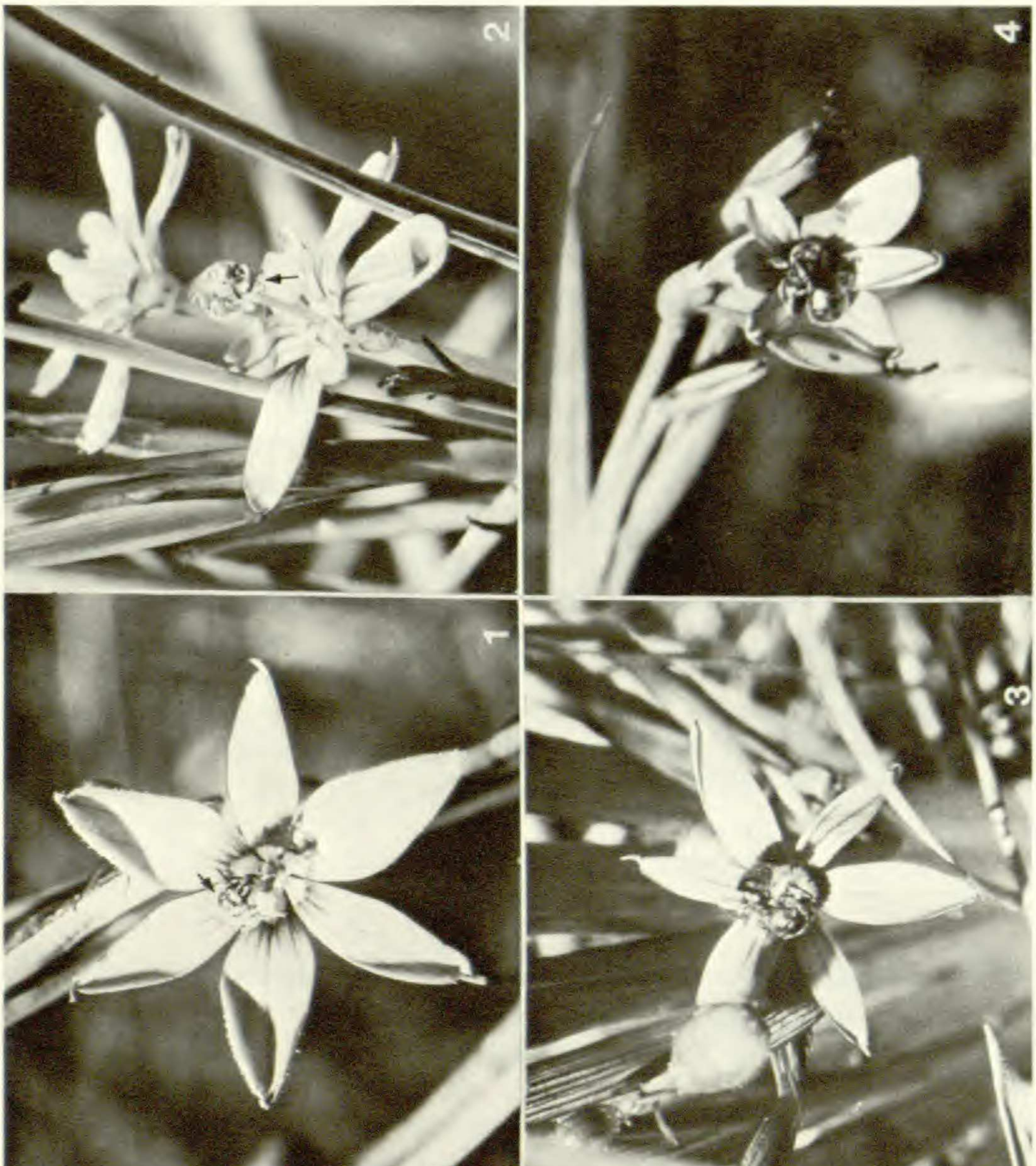
The second population was studied in Jonathan Dickenson State Park, Martin County. *Augochlorella* was not observed and few *Anthidiellum* visited the flowers. The *Anthidiellum* was the same species visiting the Palm Beach County population and exhibited the same behavior. The major difference in behavior was that the individuals in Martin County were extremely nervous.

The common visitor to this population was *Dialictus nymphalis* Smith. These small bees were numerous, and several were usually active at the same time. Because of their small size they landed on the tepals, then climbed onto the staminal column (FIGURES 1 and 2). The bees were observed gathering pollen only; however, visits to nearby *Polygonella gracilis* were apparently for nectar. As with *Augochlorella*, pollen was stored on the scopae of the posterior legs.

The details here described were obtained in 1970. Subsequent observations in 1971 and 1972 substantiate the original data. No other species have been observed visiting the flowers of this population of *Sisyrinchium solstitiale*.

All the data indicate that these three bee species are effective pollinators. Each exhibits a different behavior while on the flowers, but all contact stamens and stigmas on every flower visited. It was not unusual for bees to fly from plant to plant and cross-pollination could easily have been accomplished.

In the spring of 1971 several populations of various species of *Sisyrinchium* were studied. These populations ranged from Alachua County




FIGURES 1 and 2. **Dialictus nymphalis:** 1, bee climbing from the tepals of *Sisyrinchium solstitiale* onto the staminal column; 2, bee collecting pollen on the staminal column of *S. solstitiale*. FIGURES 3 and 4. **Augochlorella gratiosa:** 3, bee gathering pollen from *S. solstitiale*; 4, bee taking nectar from *S. solstitiale*.

south to Broward County. In only one of these spring flowering populations was a common visitor shared with the fall populations. A population of *S. miamiense* Bicknell (*S. atlanticum* sensu Long & Lakela, 1971) in Broward County was visited by *Augochlorella gratiosa*; pollination was apparently accomplished but only one individual was seen. The plants were also visited briefly on two days by *Anthidiellum notatum rufimaculatum*; on neither occasion was the bee observed to land on the flowers. The visit by *Anthidiellum* appeared to be only an inspection of the blue flowers.

## CYTOLOGY

Both *Sisyrinchium solstitiale* and *S. xerophyllum* belong to *Sisyrinchium* section BERMUDIANA, which has blue and white flowers associated with an undivided staminal column. Species presently studied in this section have a base chromosome number of $x = 8$ (Bowden, 1945; Böcher & Larson, 1950; Lewis & Oliver, 1961; Oliver & Lewis, 1962; Böcher, 1966; Oliver, 1966; Ingram, 1967; Taylor & Mulligan, 1968; Mosquin, 1970). Polyploids and a single diploid have been reported; the majority of the species are tetraploids.

Plants of *S. solstitiale* were grown in St. Louis, Missouri, from seed collected in Florida. Root tips were pretreated with low temperatures (18 hours at 1–4° C) before chromosome squashes were made. The chromosome number for *S. solstitiale* is $2n = 32$. Voucher: **Florida.** Palm Beach Co., Boca Raton, *Austin 4276* (FAU).

Mosquin (1970) reported compatibility and selfing in a bagging experiment on what we assume to be a 12-ploid population of *S. montanum* Greene. In contrast to this we found *S. solstitiale* to be self-incompatible. Seed set could be accomplished only by cross pollination. Self-incompatibility is also common in other tetraploid *Sisyrinchium* species from the Pacific Northwestern United States (Douglas Henderson, pers. comm.). We have not seen evidence of gene exchange between this species and any other.

## DISCUSSION

We suggest that the ancestral form of the two species of *Sisyrinchium* we have studied occurred in the lower southeastern United States at the beginning of the Pleistocene. During the changing sea levels of the glacial and interglacial stages, various populations of the ancestral form became isolated. Each of the modern species resulted from evolutionary shifts in preference to habitat, flowering season, flowering time of day, pollinators, etc. *Sisyrinchium xerophyllum* maintained a more conservative biology by retaining the temperate spring flowering characteristics and living in relatively mesic conditions in the High Pinelands.

*Sisyrinchium solstitiale* was perhaps isolated from the other forms on the Pleistocene islands. The Scrub forests of the Ocala Ridge and farther south have been considered the sites of evolution for several plant and animal species (Carr, 1940; Neill, 1957). Since *S. solstitiale* now prefers this habitat, it seems reasonable to assume that this species may also have evolved with the other Scrub species. Because conditions are xeric in the Scrub, spring flowering plants were probably at a disadvantage since the spring is usually dry. A selection toward flowering in the late summer and early fall, when rain is more abundant, would have resulted in survival and reproduction being more easily accomplished. This shift to late flowering parallels similar shifts in Mexico.

If this interpretation is correct, *Sisyrinchium solstitiale* can be con-

sidered a recently evolved species. Almost certainly its closest relative is *S. xerophyllum*. Because their habitat and flowering seasons rarely overlap, there is a strong tendency to consider the populations as two separate gene pools.

## ACKNOWLEDGMENTS

For this study we have examined materials from the herbaria at A, FAU, FLAS, FSU, GH, MO, SMU, UNC, USF, and US (abbreviations follow Index Herbariorum, Ed. 5, Reg. Veg. 31. 1964). We are grateful for the assistance given by curators and staff members of these herbaria. W. H. Mahler graciously furnished space at the Southern Methodist University for this study during most of the summer of 1972. B. G. Schubert and K. R. Robertson gave many helpful suggestions on the original manuscript.

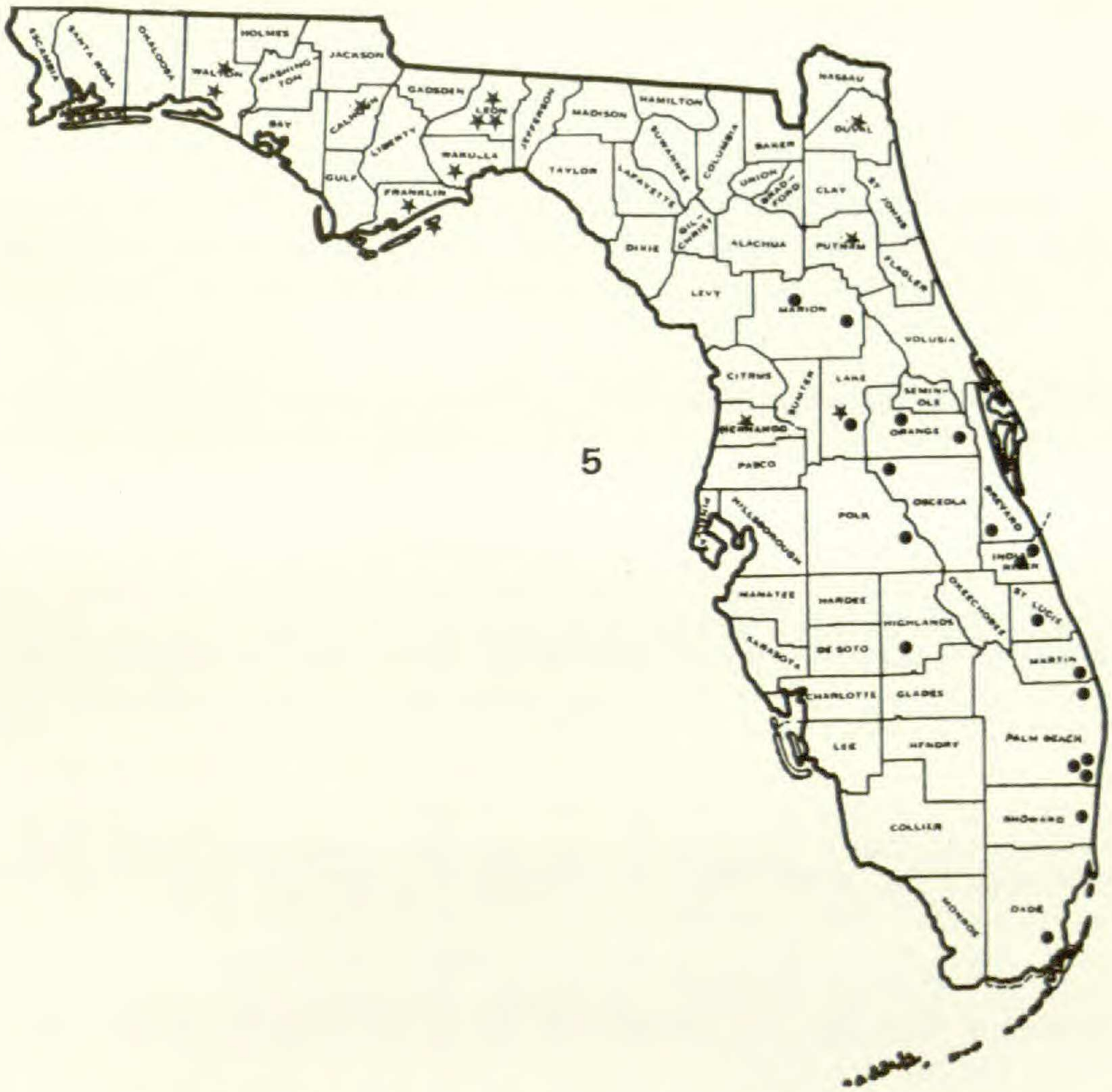



FIGURE 5. Distribution of *Sisyrinchium solstitiale* (solid dots) and *S. xerophyllum* (stars).

## DOCUMENTATION

1. **Sisyrinchium xerophyllum** Greene, Pittonia **4**: 32. 1899. HOLOTYPE: *Nash 133* (ND–G); (GH, MO, NY, US, isotypes).

REPRESENTATIVE SPECIMENS:

**Florida.** CALHOUN Co.: 10 May 1964, *McDaniels 4428* (FSU). FRANKLIN Co.: 24 Mar. 1970, *Godfrey 69316* (FSU); 23 Mar. 1961, *Kral 118313B* (FSU); *Godfrey 53124* (NY). GADSON Co.: 19 Mar. 1966, *McDaniels 7286* (FSU). HERNANDO Co.: 19 Mar. 1958, *Cooley & Monachino 5659* (FSU). LAKE Co.: 20 Mar. 1894, *Nash 133* (MO, ND–G, NY, US). LEON Co.: 28 Apr. 1964, *Godfrey 63578* (FSU); 30 Mar. 1957, *Kral 4747* (SMU). PUTNAM Co.: Apr. 1961, *Gillis 4348* (FSU). WAKULLA Co.: 1 Apr. 1934, *Hunnewell 13094* (GH). WALTON Co.: 17 Apr. 1958, *Godfrey 56629* (FSU, SMU); 6 Apr. 1957, *Godfrey 55491* (FSU, GH, NY, SMU).

2. **Sisyrinchium solstitiale** Bicknell, Bull. Torrey Bot. Club **26**: 219. 1899. TYPE: *Nash*. ". . . high pine land at Eustis, Lake Co., Florida, Aug. 10, 1894, the first flowers just opened. Type in herbarium Geo. V. Nash" (presumably NY, not located).

REPRESENTATIVE SPECIMENS:

**Florida.** BREVARD Co.: 15 Jan. 1903, *Fredholm 5698* (GH, US). BROWARD Co.: 19–25 Nov. 1903, *Small & Carter 1228* (NY). DADE Co.: 30 Nov. 1912, *Small 4008* (NY); 30 Jan. 1930, *Moldenke 300A* (NY). HIGHLANDS Co.: 17 Oct. 1967, *Beckner 788* (FSU, GH, USF); 22 Aug. 1971, *Godfrey 70805* (FSU); 20 Sept. 1964, *Kral 22893* (SMU); 27 Dec. 1924, *Small 11573* (NY); 4–5 Sept. 1934, *Small & West s.n.* (NY); 28 Nov. 1959, *Ray 9628* (FSU, GH, USF); 7 Oct. 1960, *Ray et al. 10348* (USF); 2 Sept. 1954, *Shanks et al. 17959* (SMU); 7 Dec. 1925, *Small 12728* (NY, UNC, USF). INDIAN RIVER Co.: 26 June 1957, *Kral 5073* (SMU). MARION Co.: 12 Sept. 1929, *O'Neill 7828* (FSU, US); 12 Oct. 1964, *Ward 4192* (FLAS, FSU, GH, USF). MARTIN Co.: 23 July 1959, *Ward & Ward 1575* (FLAS, FSU). ORANGE Co.: 26 Oct. 1959, *Craighead s.n.* (FSU); 20 Dec. 1949, *Shallert 5442* (SMU). OSCEOLA Co.: 14 Oct. 1960, *Putnam s.n.* (USF); 14 Oct. 1960, *Ray et al. 10462* (USF). PALM BEACH Co.: 25 Oct. 1970, *Austin 4276* (FAU); 20 Dec. 1968, *Churchill s.n.* (SMU). POLK Co.: 11 Nov. 1960, *Lakela 23592* (FSU). ST. LUCIE Co.: 7 Dec. 1920, *Small & DeWinkler 9728* (GH, SMU, UNC, US). COUNTY UNKNOWN: S. Florida, *Binney s.n.* (GH) [annotated by Bicknell in 1899; the only specimen of this species annotated by the original author that we have seen.]

## LITERATURE CITED

BICKNELL, E. P. Studies in *Sisyrinchium* — I: Sixteen new species from the southern states. Bull. Torrey Bot. Club **26**: 217–231. 1899.

———. *Sisyrinchium*. *In*: J. K. SMALL, Flora of the Southeastern United States, 293–304. 1903.

BÖCHER, T. W. Experimental and cytological studies on plant species. X. *Sisyrinchium* with special reference to the Greenland representative. Bot. Tidsskr. **61**: 273–290. 1966.

——— & K. LARSEN. Chromosome numbers of some arctic or boreal flowering plants. Medd. Grønl. **147**(6): 1–32. 1950.

BOWDEN, W. M. A list of chromosome numbers in higher plants. I. Acanthaceae to Myrtaceae. Am. Jour. Bot. **32**: 81–92. 1945.

CARR, A. F. A contribution to the herpetology of Florida. Univ. Florida Publ. Biol. **3**: 1–118. 1940.

COOK, C. W. Geology of Florida. Florida Geol. Surv. Geol. Bull. **29**: 1–339. 1945.

DAVIS, J. H., JR. The natural features of southern Florida. Florida Geol. Surv. Geol. Bull. **25**: 311 pp. 3 maps. 1943.

INGRAM, R. On the identity of the Irish populations of *Sisyrinchium*. Watsonia **6**: 283–289. 1967.

LAKELA, O., & F. C. CRAIGHEAD. Annotated checklist of the vascular plants of Collier, Dade and Monroe Counties, Florida. viii + 95 pp. Fairchild Trop. Gard. & Univ. Miami Press, Coral Gables. 1965.

LEWIS, W. H., & R. L. OLIVER. Meiotic chromosomes in six Texas and Mexican *Nemastylis* and *Sisyrinchium* (Iridaceae). Southwest. Nat. **6**: 45, 46. 1961.

LONG, R. W., & O. LAKELA. A Flora of Tropical Florida. xviii + 962 pp. Univ. Miami Press, Coral Gables. 1971.

MOSQUIN, T. M. Chromosome numbers and a proposal for classification in *Sisyrinchium* (Iridaceae). Madroño **20**: 269–275. 1970.

NEILL, W. T. Historical biogeography of present-day Florida. Bull. Florida State Mus. **2**: 175–220. 1957.

OLIVER, R. L. Chromosome numbers in phanerogams. I. Ann. Missouri Bot. Gard. **53**: 100–103. 1966.

——— & W. H. LEWIS. Chromosome numbers of *Sisyrinchium* (Iridaceae) in Eastern North America. Sida **1**: 43–48. 1962.

TAYLOR, R. L., & G. A. MULLIGAN. Flora of the Queen Charlotte Islands. Part 2. Cytological aspects of the vascular plants. Canada, Dept. Agric. Monogr. 4(2). x + 148 pp. 1968.

WARD, D. B. Checklist of the Vascular Flora of Florida. I. Bull. Florida Agric. Exper. Sta. **762**: 1–72. 1968.

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